ENVIRONMENTAL REACTIONS OF PHRYNOSOMA[1]

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I. INTRODUCTION

1. *General Distribution.*—The horned lizards, more familiarly known as the "horned toads," of the southwestern portion of the United States and the northern states of Mexico form a very distinct group of the family Iguanidæ. Unlike most other comparatively large reptilian genera, this particular genus (*Phrynosoma*) is limited to a very special environment, and it is only in a region of relative aridity that these animals find a favorable habitat. Within the limits set by the above condition the specific habitats of the various species and varieties of the genus vary greatly, ranging all the way from the extreme aridity and great heat of Death Valley in southern California (*Phrynosoma calidiarum* Cope) to the comparative moisture and cold of the northern Rockies (*Phrynosoma douglassii* Bell and varieties). The species especially discussed in this paper are all found in the Southwest, under varying environmental conditions.

Phrynosoma modestum, the specimens of which were taken near Albuquerque, New Mexico, close to the lower edge of the "mesa" or clinoplane region, at an altitude of about 1,700 meters, is distributed throughout New Mexico, and to a certain extent in the adjoining states, wherever conditions are similar to those in the above typical habitat. The rainfall here averages about 30 cm. annually, while the yearly evaporation from a free water surface is in the neighborhood of 200 cm. The soil is

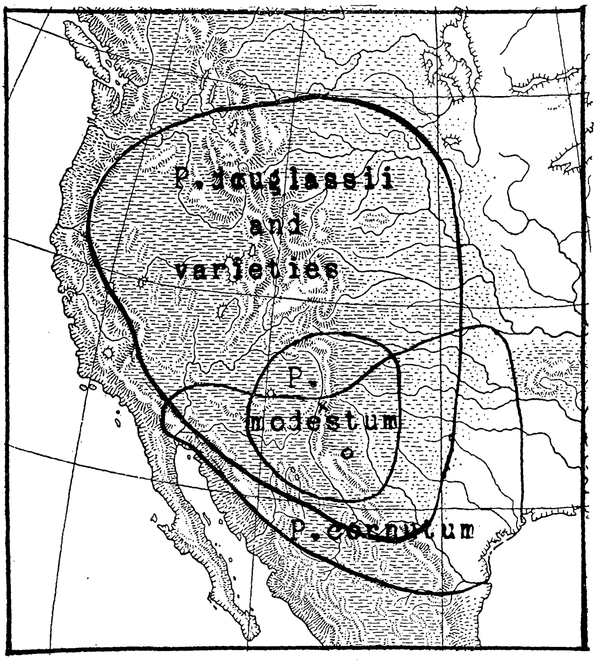
[1] Contribution from the Zoological Laboratory of the University of Illinois.

rather loose and friable, consisting principally of "Tijeras fine sandy loam" and containing, near the surface, a relatively large proportion of fine angular gravel and wind-blown sand. The color is a yellowish or yellowish brown. The vegetation is sparse, consisting of scattered grasses, *Chrysothamnus, Gutierrezia, Salsola, Yucca*, etc. This species is not found in the adjoining valley of the Rio Grande, nor in the mountains (Sandias) which border the "mesa" on the east (2,200 meters and above), where moister conditions prevail. In the mountains the rainfall is probably twice as great, on the average, as on the "mesa," although accurate data are not available, and the evaporation is much less, due to the lower temperatures which prevail. In the valley the water table is very near the surface of the soil (actual soil surface or above to 5 meters below the surface). Standing water is not found on the clinoplane except after very heavy rains, which sometimes fail for months.

Phrynosoma douglassii ornatissimum, specimens of which were obtained with the above, has a much less restricted habitat, both locally and regionally. It is distributed over a great deal of the eastern slope of the Rocky Mountains, even as far north as Canada, and, locally, extends into both of the regions described above as bordering on the clinoplane. It is, indeed, more abundant in either of these than in the clinoplane region between, indicating that the determining factor in the distribution in this case is similar in the lower valley and on the mountain side. As mentioned above, the aridity of these two regions is much less than that of the clinoplane. The soil differences are also marked, in that the moister soils are more dense and contain more humus, derived from the more abundant vegetation. However, the variation in both regions is very great, from heavy clay to fine sand in the valley and from native rock to fine sand in the mountain.

Phrynosoma cornutum does not occur in the same local area as that occupied by the species previously mentioned,

although it also is of wide distribution. This species is found throughout Texas and eastern and southern New Mexico, and has been reported from Nebraska, Arkansas, etc. In general, it appears to inhabit regions in which the mean summer temperature is slightly higher than that



Map showing the approximate geographical distribution of the species discussed in this paper.

required by the other two species. The specimens here considered were obtained at Alamogordo, in the Otero Basin, New Mexico, where the mean temperature is higher by about 5° C. than at Albuquerque.

2. *General Habits.*—The general habits of the three species here considered are much the same, so no separate description will be attempted. The following discussion will apply, perhaps, more accurately to *Phrynosoma modestum* than to either of the other species, but will, in general, be true of all. They are not, essentially, heat-loving animals, although tolerant of desert condi-

tions. They are found more abundantly during the earlier summer months, and during the autumnal rainy season, when the aerial temperature does not exceed 32° C. During these periods the animals move about actively all day, spending the night in protected nooks under vegetation, in the burrows of other animals, or buried beneath the surface of the soil. As the daily maximum temperature becomes greater they are to be found only in the early morning and in the later afternoon when the heat is less intense. During the heated part of the day the lizard is at rest, almost if not quite buried under the superficial layers of the soil. This position is reached in a characteristic manner. The snout is directed downward and moved rapidly from side to side, the body extremely flattened, while the legs take part in a rapid horizontally clawing movement. The net result of this series of movements is to cover the animal with the loose soil, the depth varying according to the temperature, the character of the soil, and other external conditions, as well as the individual. The same method of burrowing is employed in preparation for hibernation, when the animal may bury itself under several inches of loose soil. In attempting to escape from enemies, other lizards have been observed to dig in a similar manner, and it is probable that *Phrynosoma* also escapes in this way.

3. *Food Relations.*—The food consists of various insects with which the animals come into contact, ants being more readily eaten by the smaller individuals and beetles (*Eleodiini*) forming a considerable portion of the diet of the larger ones. No food is taken unless it is living or at least moving. Sand grains set in motion by a heavy wind or otherwise are often snapped up, and sand grains are accordingly found in the feces.

4. *Water Relations.*—None of the species of *Phrynosoma* have been observed by the writer to drink water, and it is doubtful if water, independent of that contained in the insect food, is ever ingested. Many individuals are found in situations where there is never any standing

water except after the very infrequent heavy rains. Very little water is excreted ordinarily, as when fed on ants, beetles, etc., the feces are eliminated as a dry mass containing practically no water, and the urine is composed of an equally dry mass largely made up of crystals of uric acid. When fed on a moist diet, such as grasshopper nymphs from a moist habitat, the feces become softer and are often accompanied by a considerable amount of mucilaginous liquid. The urine, however, remains as usual. The idea that the excretion of waste nitrogen as uric acid is an adaptation on the part of the Reptilia for life in arid regions is well borne out by the conditions in these animals. Urinary analyses made by the writer in the laboratory of physiological chemistry of the University of Illinois give the following results (1917*b*):

Constituents	Milligrams per gram
Total nitrogen (N_2)	260.0
Ammonia nitrogen	1.4
Urea nitrogen	0.0
Uric acid	765.0
Uric acid nitrogen	255.0
Ash	87.5
Phosphorus as P_2O_5	3.5

It will be observed that uric acid accounts for practically all of the nitrogen contained in the urine and that urea is entirely absent. In this respect the urine of the horned lizard differs from that of the aquatic and semiaquatic reptiles, which contains a considerable amount of urea, as does that of birds, another group in which the uric acid content is high.

5. *Reproduction.*—It is in connection with *Phrynosoma cornutum* that the long-disputed question as to the viviparity or oviparity of the members of this genus may be opened again. Cope (1898) states that *Phrynosoma* is oviparous, which is denied by Ditmars (1908) and Watson (1911), the latter of whom bases his statement on observations of *P. douglassii.* On July 5, 1917, some twenty specimens of *P. cornutum* were received at the vivarium

of the University of Illinois from Alamogordo, New Mexico, and placed in a sand-bottomed wire screen cage. On July 7, between 11 A.M. and 1 P.M., twenty-three eggs were deposited in the sand on the bottom of the cage. The eggs were about 1 cm. in length, ovoid in shape, and covered with a grayish-white shell of leathery texture. Some were opened and found to contain living embryos of about 2 mm. length. Several times thereafter, during a period of two weeks, eggs were found in the cage, always lots of about twenty. The deposition of the eggs was never observed. None of the eggs hatched, although living embryos were found in eggs opened a week after deposition. Such embryos were about 6 mm. in length. *P. douglassii* has not been observed to lay eggs, although a few eggs of *P. modestum* were discovered in the cage in which these animals were kept. These were found in small numbers only and differed from those just described in being light yellow in color and having no leathery shell. They were probably abortive. As the observations of Watson and Ditmars appear to be well founded, it is possible that the genus is divided with respect to the retention or deposition of the eggs, or that in the same species different conditions may alter the length of time the egg is retained in the maternal body, as is the case among the adders.

II. ENVIRONMENTAL FACTORS

As has been concluded (1917*a*), it is dangerous to ascribe to any one factor or group of factors the supreme rôle in determining the seasonal or general distribution of a species. These factors are certainly not the same for all species even in the same environment, and before definite conclusions can be drawn a careful analysis of the habitat must be made, and experimental data must be obtained as to the reactions of the animals in gradients involving the factors capable of variation. Unfortunately, it is not possible or practicable to construct effective

gradients involving all environmental conditions, and in such cases we must rely on careful observation and analysis. Such a review as has just been given of the habitat and habits of the horned lizards may indicate to us the probable external conditions variations of which are of importance in the daily and seasonal life of the individual and of the species. The following are the most apparent of such external conditions:

1. Temperature.
    - (*a*) Air.
    - (*b*) Soil.
    - (*c*) Maxima and minima.
2. Water.
    - (*a*) Relative humidity and evaporating power of air.
    - (*b*) Soil moisture.
    - (*c*) Food in relation to its water content.
3. Soil.
    - (*a*) Texture as influenced by
        1. Composition.
        2. Moisture content.
        3. Vegetation.
    - (*b*) Color.
4. Food.
    - (*a*) Character.
    - (*b*) Abundance or scarcity.
5. Light.
    - (*a*) Quality.
    - (*b*) Quantity.
    - (*c*) Rhythm.

In the natural habitat it is rare that one of the above conditions varies without an accompanying variation in one or more of the others; for example, a variation in temperature of the air is accompanied by a variation in the relative humidity and in the evaporating power of the air, and may be followed by an alteration of soil temperature and soil moisture, as well as soil texture. Thus it is difficult to consider these conditions separately.

1. *Temperature.*—That temperature affects profoundly the daily life of the animal and limits its activities is shown by the relation of daily variation in temperature to the change from diurnal to crepuscular habit and to the burrowing activities initiated by high or low temperatures. Minimum temperature is probably associated most closely with the phenomena of hibernation. According to Bachmetjew (1901) the minimum winter temperature which can be survived by hibernating insects depends on the degree of elimination of water from the tissues and the consequent lowering of the freezing point of the body fluids. Tower (1917) states that in the case of potato beetles those animals acclimated to desert conditions (retention of water) are killed at higher temperatures than those of a more humid climate. In the experiments to be described gradients in air temperature and in soil temperature (substratum temperature) were established and the reactions of animals in such gradients were recorded.

2. *Water.*—The water relation must always be important in an animal adapted to arid conditions, even though this relation may seem to be negative. As indicated by the examination of excreta and observation of the water relations of *Phrynosoma* it would appear that the absence of water as such would not have a limiting effect on the distribution of the animals. It is probably necessary, however, that a certain minimum amount of water be supplied in the food, and that the evaporating power of the air must not exceed a certain maximum for any great length of time. It is to be doubted that any vertebrate may subsist indefinitely without some small water supply in addition to metabolic water. As shown in previous experiments (1917*a*), the reaction of *Phrynosoma* in a gradient of the evaporating power of air is not definite unless the gradient be very steep. Daily variation in the normal habitat is very large.

3. *Soil.*—The apparent importance of the burrowing reaction in the life history of the members of this genus

points to a corresponding importance of the texture of the soil. Evidently this must be such as to render the success of the burrowing reaction comparatively easy, a condition which is met only in soils of a low moisture content, and little humus, containing a considerable amount of loosely aggregated particles of sand or fine gravel. In a heavy clay or loam it would be impossible for the animal to burrow deep enough to get below the zone of killing temperatures during hibernation. This would also be impossible in a compact sod. Unfortunately, the problem of the soil relation involves an extensive seasonal study which, so far, it has been impossible to carry out.

While the color and markings of the animals vary with the individual and the species, and the color of the individual changes from time to time, it may be said in general that the color of the horned lizard is very similar to that of the soil of its normal habitat. Experiments of the author and others have shown that high temperature, darkness or high evaporating power of the air causes a centripetal movement of the melanophoric pigment, while the opposite conditions cause a darkening. Thus, in general, individuals observed after a rain are darker in color than at other times. The soil is also darker when wet, which might lead the observer to suppose that the change had taken place as a direct adjustment to the color change of the substratum, while the actual cause is the change in the evaporating power of the air. Within the limits of the conditions of the habitat, variations in the evaporating power of the air are the most potent factors in the production of color changes. No direct connection between the color of the animal and that of the substratum has been verified experimentally by the author. Redfield (1917), in a recently published paper on the color changes in *Phrynosoma cornutum,* has stated that there is a direct approximation of the color of the animal to that of the substratum, and that the light rays reaching the retina form the stimulus for such changes. The mechanism for

the approximation of the color of the animal to that of the substratum is, according to Redfield, subordinate to the daily rhythm of color change occasioned by changes in light and temperature, and to changes brought about by the emotional condition of the animal.

4. *Food.*—An adequate study of this factor would require much more extended observation than has been possible. Some suggestions as to the character of food required have been made above.

5. *Light.*—An estimation of the effect of light of varying intensity and quality in the natural habitat would be very difficult, but it is probable that the relations of light in the life of such animals have been greatly underestimated. Experiments with a gradient of the color of light are included here.

III. Experimental Results

1. *Air Temperature Gradients.*—Two series of experiments were performed in which air varying in temperature was passed across the experimental cage previously (1917*a*) described. In the first series the air passing across one third of the cage was heated to a temperature of about 38° by being passed through coils immersed in hot water, that passing across the next third was heated to about 33°, while the remaining third was supplied with air at about 29°. The air was unmodified except as to temperature and the rate of flow was the same in each case. Typical results of this series (*Phrynosoma modestum* only) are shown statistically in Table I.

In the second series the air for the hottest third was heated to a temperature in the neighborhood of 50°, which is about the maximum soil surface temperature on unprotected sand exposed to the direct rays of the sun. This temperature was obtained by passing the air through heated iron pipes. A medium temperature was obtained by passing the air through coils immersed in hot water, as above, while the lowest temperature was that of the

TABLE I

EXPERIMENT 34. SHOWING THE REACTIONS OF *Phrynosoma modestum* IN AN AIR TEMPERATURE GRADIENT

Ten animals were placed in the cage, and observations of their position taken at one-minute intervals. The temperatures taken at intervals along the cage are indicated at the heads of the respective columns.

Minutes	Temperatures					
	Experiment 34*a*			Experiment 34*b*		
	29°	33°	38°	38°	33°	29°
1	3	3	4	3	4	3
2	4	2	4	3	5	2
3	4	2	4	3	6	1
4	4	2	4	4	4	2
5	3	2	5	4	4	2
6	3	2	5	4	5	1
7	3	4	3	4	5	1
8	3	4	3	4	5	1
9	3	4	3	4	5	1
10	3	4	3	4	5	1
11	3	4	3	4	5	1
12	4	3	3	4	5	1
13	2	4	4	4	5	1
14	2	4	4	4	4	2
15	2	4	4	3	5	2
16	2	4	4	3	5	2
17	2	4	4	3	5	2
18	2	3	5	4	5	1
19	2	3	5	4	5	1
20	2	3	5	4	5	1
21	2	3	5	5	4	1
22	1	5	4	5	4	1
23	1	5	4	5	4	1
24	1	5	4	4	5	1
25	1	5	4	3	6	1
26	1	4	5	3	6	1
27	1	4	5	3	6	1
28	1	4	5	3	6	1
29	1	4	5	3	6	1
30	1	4	5	3	6	1

unmodified air, about 30°. These temperatures varied somewhat in the various experiments, as shown by the records, but were fairly constant throughout a single experimental period.

The records of Experiments 34*a* and 34*b* show, for *Phrynosoma modestum*, that the optimum air temperature is in the neighborhood of 35° or 36°. The graphic records of Experiments 86 and 88 (Pl. I) show similar results. It will be noticed in the record of the former

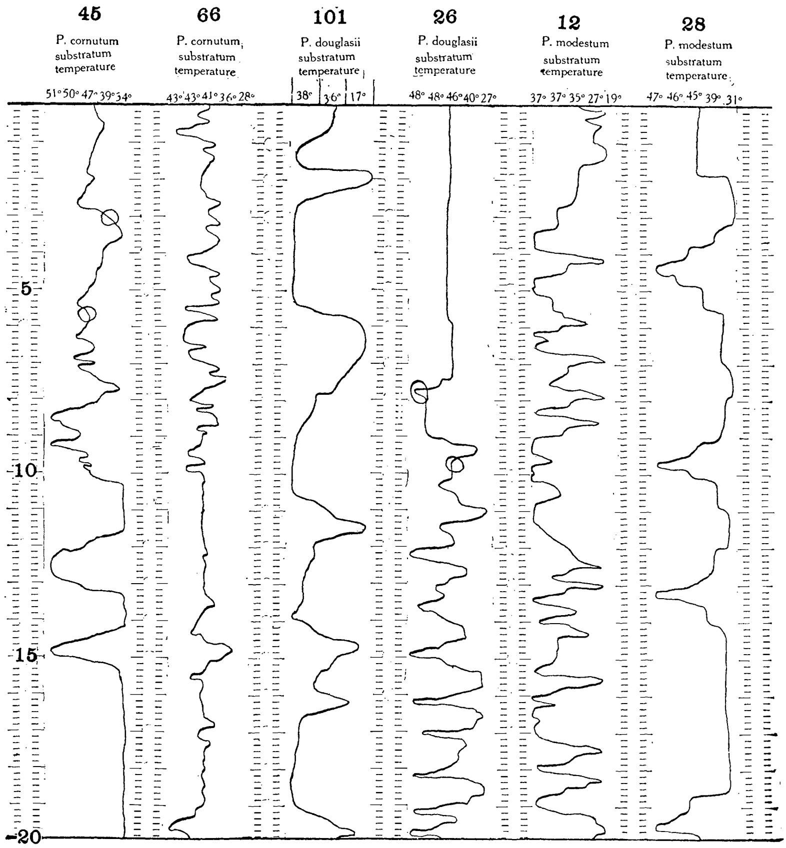
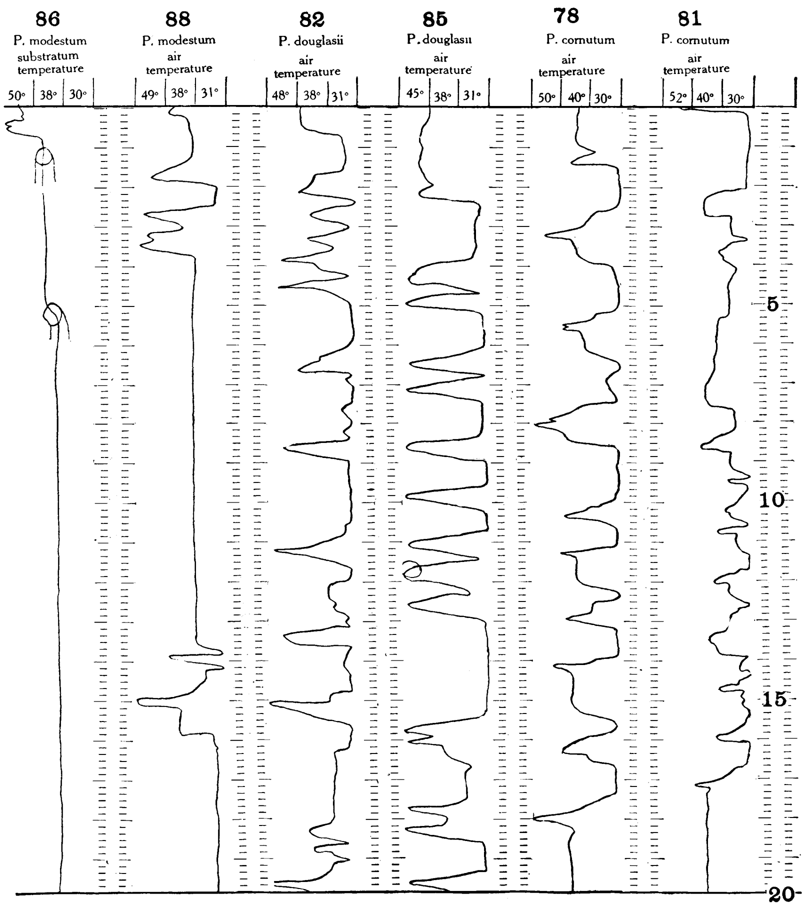


PLATE I. Illustrating the reactions of *Phrynosoma* in gradients of air temperature and substratum temperature. Experiments No. 45, 66, 101, 26, 12, 28, 86, 88, 82, 85, 78, 81.

In the chart, each section between the numbered scales represents the record of a twenty-minute experiment, the distance between the scales representing the length of the cage, and the vertical length of the chart the time, twenty minutes, each division on the scale representing ten seconds. The curve represents the movements of the animal under observation, and as the time component is vertical and the space component horizontal, the parts of the curve most nearly horizontal represent the most rapid movements, while the vertical parts of the curve indicate that the animal remained in the same position during the length of time indicated on the adjacent scale. The character of the experiment is in each case noted above the graph, as is the temperature of the various parts of the cage. In some the temperature was taken in five places along the cage and in others in only three places, as indicated. The circles found in the graphic records of certain experiments indicate that the animal attempted to burrow at the times indicated.

Controls, *i. e.,* experiments in which all portions of the cage were at the same temperature, were carried out in all cases, but the regular curves obtained have been omitted to save space.

Experiment 45.—For the first two minutes the animal was comparatively quiet, and after the close of this period moved toward the hot end of the cage, to return immediately, and then attempted to burrow. Just after the fifth minute the animal again moved toward the higher temperature and again burrowed. Thereafter the movements were of greater amplitude but less frequent, until the animal finally came to rest near the cooler end of the cage, where it remained until the end of the experimental period.



Experiment 66 shows a record of almost the same character, except that all movements were of lesser amplitude.

Experiment 101.—Phrynosoma douglassii here remained for the greater part of the time at a temperature of about 38°, making infrequent excursions into the region of lower temperature.

Experiment 26.—Same species as above. The temperatures here were higher, and the animal avoided the highest temperatures.

Experiments 12 and 28 show results similar to the two just preceding, in one the avoidance of low temperatures and in the other the avoidance of higher temperatures.

Experiment 86.—This is the record of the movements of a very sluggish individual, which burrowed twice at a temperature a little above that chosen by other members of the species.

Experiment 88.—This animal showed alternate periods of rest at an optimum temperature and activity involving incursions into both temperature extremes represented in the gradient.

Experiments 82 and 85 are good examples of the type in which there is great activity, but very short stays in the unfavorable temperatures.

Experiment 78.—This record shows avoidance and turning away from the higher temperatures. The farther the animal penetrated into the high temperature area before turning, the longer was the subsequent inactive period in the region of optimum temperature.

Experiment 81.—This animal was very sensitive to the higher temperatures and never reached the hot end, although very active at times.

that the animal burrowed, first at a temperature of about 38° and later at a slightly lower temperature (indicated by the circles in the first and sixth minutes of the record). This burrowing reaction was found to take place very often, throughout the whole series, usually at the upper limit of the optimum temperature range. This agrees with the phenomena observed in the field, of burrowing as the air temperature rises in the course of the day.

Phrynosoma douglassii, as shown in the graphic records of Experiments 82 and 85 (Pl. I), seems to choose a somewhat lower temperature, between 30° and 35°, although there is a considerable amount of individual variation.

Phrynosoma cornutum, the behavior of which in the gradient is illustrated by the records of Experiments 78 and 81 (Pl. I), appears to show a preference for a temperature slightly higher than that shown by the other species.

2. *Substratum Temperature Gradients.*—For the purpose of establishing this gradient the cage was placed in a water bath so arranged that hot water flowed into the latter at one end and cold water at the other, the water being directed backward and forward beneath the cage, and running out near the center, in such a manner as to produce a gradient in the temperature of the cage bottom. The temperature of the substratum was taken at intervals along the edge of the cage by thermometers whose bulbs were just covered by the sand in the bottom.

The statistical records of Experiments 43, 126 and 127 (Table II) show an optimum substratum temperature for *Phrynosoma modestum* of about 40°, or about 5° higher than the optimum air temperature for the same species. In this species the response to changes of temperature of the substratum is very definite, and by varying the temperatures of the gradient, the animals can be driven repeatedly from one end of the cage to the other as the temperature is raised or lowered. The lizards often burrowed at or near the upper limit of the optimum temperature, and, less often, at the temperatures below the

optimum. The graphic records of Experiments 10 and 28 (Pl. I) show similar results.

TABLE II

EXPERIMENTS 43 AND 127. SHOWING THE REACTIONS OF *Phrynosoma modestum* IN A GRADIENT OF THE TEMPERATURE OF THE SUBSTRATUM

The method of recording is the same as that employed in Table I.

Minutes	Temperatures					
	Experiment 43			Experiment 127		
	45°	41°	36°	25°	40°	52°
1	2	4	2	2	6	2
2	2	4	2	1 *1**	8	0
3	2	4	2	1 *1*	8	0
4	2	5	1	*1*	8	1
5	2	5	1	*1*	8	1
6	2	4	2	*1*	8	1
7	2	5	1	*1*	8	1
8	3	4	1	*1*	9	0
9	1	6	1	*1*	9	0
10	1	5	2	*1*	9	0
11	1	5	2	*1*	*1** 8	0
12	2	5	1	*1*	*1* 8	0
13	2	5	1			
14	1	6	1			
15	1	5	2			
16	1	5	2			
17	0	6	2			
18	0	6	2			
19	0	6	2			
20	0	7	1			

* The individuals indicated by the *italic numerals* burrowed in the space indicated.

The individuals of *Phrynosoma douglassii* gave practically the same figures for the optimum substratum temperature. The graphic records of Experiments 101 and 26 indicate the behavior of this animal in the gradient. Statistical records of the behavior of *Phrynosoma douglassii* and *Phrynosoma cornutum* in this gradient were not made, because of the size of the animals, which prevented the introduction of any number into the cage at the same time.

Phrynosoma cornutum, as illustrated by the records of Experiments 45 and 66 (Pl. I), chose a higher substratum temperature than either of the other species, averaging nearly five degrees above that shown by the other curves.

In summing up the results of the air temperature and substratum temperature experiments (over one hundred) in relation to those of the evaporation gradient previously reported (1917*a*), it is found that the animals choose conditions which are very near the normal conditions in the usual habitat at the time of the greatest activity. These conditions represent the optimum for the animals. For example, as reported in a previous paper, the evaporation optimum for *Phrynosoma modestum* appears to be near 3 c.c. per hour, as measured by the standard atmometer, which is very near the average outdoor evaporation as observed in the natural habitat of the animal at the season and at the time of day when the animal is most active. If the temperature under such conditions be observed, it will be found that the average atmospheric temperature, 1 cm. from the surface of the soil, in the sun, is in the neighborhood of 35°, and that of the surface layer of the soil about 40°. These temperatures vary greatly, of course, with other features of the weather, such as air movements, clouds, etc., but the above figures represent a normal condition. Of the variables mentioned here, substratum temperature has much the greatest effect on the behavior of the animal.

3. *Moisture of Substratum Gradient.*—Although it was impossible to establish and observe an effective gradient in general soil conditions, several experiments were performed on the direct effect of a soil moisture gradient. The gradient in water content of the substratum was obtained by placing a layer of torpedo sand saturated with water on the bottom of one third of the cage, a mixture of saturated sand and dry sand in the adjoining third, and dry sand in the remainder of the cage. In none of the species observed was any marked preference for any portion of the cage exhibited. Soil moisture, as such, does not seem to affect the movements of the animals, although, in the natural habitat, the high evaporating power of the air produces a considerable degree of temperature difference between dry soil and wet soil by the

vaporization of the water from the latter. This difference was not reproduced under experimental conditions. Typical results of this series of experiments are shown in the graphs of Experiments 91 and 97 (Pl. II).

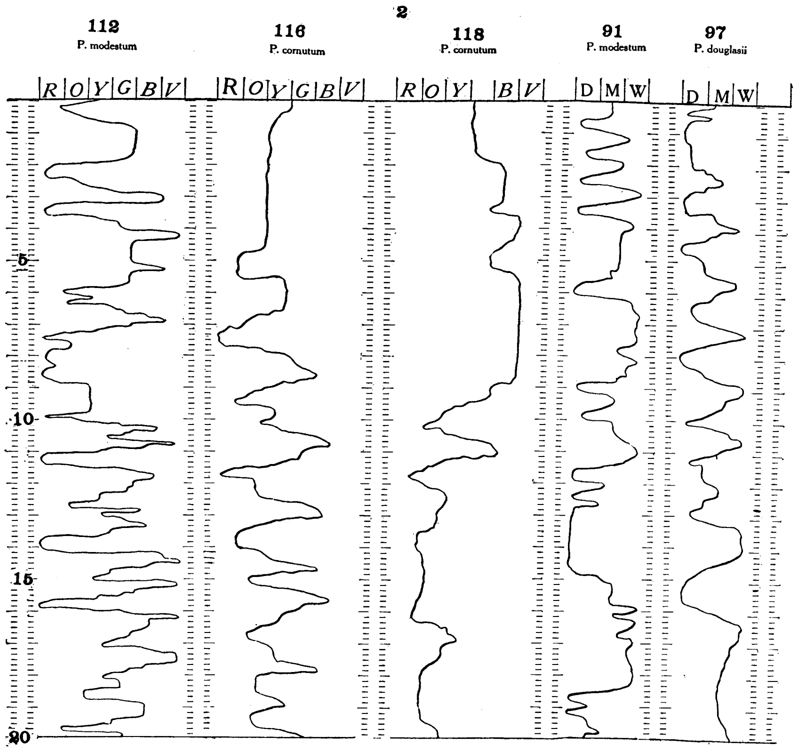


PLATE II. Illustrating the reactions of *Phrynosoma* in gradients of wavelength (color) of light and moisture of substratum. Experiments 112, 116, 118, 91 and 97.

Experiment 112.—In this and the two experiments following, the letters *R, O, Y, G, B* and *V* above the graphs represent the color of the light screen over the corresponding portion of the cage. The graphs may be interpreted in the same manner as those illustrated in Plate I. In this experiment the animal avoided the violet section, turning away from it rather quickly in each instance, The greater part of the time was spent in the green and the yellow.

Experiment 116.—This animal avoided the violet and even the blue very markedly and entered the red only twice. The optimum seems to be in the yellow and the green.

Experiment 118.—Avoidance of both the violet and the red is characteristic of this curve. This animal, however, did not avoid the blue and the orange, in which it spent a considerable amount of time.

Experiments 91 and 97.—Here the letters *D, M,* and *W* refer to dry, medium and wet thirds of the cage. The graphs show no preference for either on the part of the animal.

4. *Gradient in the Color of Light (Wave-Length).*—Although it would be difficult to estimate the effect of the various light components in the natural habitat, a series of light experiments has been included. For use as a color gradient the cage used in the other experiments was covered with an accessory lid composed of a series of six equal strips of gelatine ray filter in the principal colors (violet, blue, green, yellow, orange, red). Three forty-watt electric lamps were placed above the cage within the observation hood, so that the light was approximately equally distributed throughout the cage, each sixth being illuminated principally by rays of a narrow range of wave-length.

Experiment 112 illustrates the movements of *Phrynosoma modestum* in such a gradient. The longest rays were avoided, as well as the shortest, although the animal remained for greater lengths of time in the red section than in the violet. The optimum seems to lie in the green and the yellow.

Phrynosoma cornutum (Experiments 116 and 118, Pl. II) avoided both red and violet, with an optimum near the middle of the spectrum. *Phrynosoma douglassii* did not respond regularly and seemed little affected.

The color reactions are probably not as significant as those involving some of the other factors here considered. Direct sunlight in the arid regions contains a rather larger amount of the light of the shorter wave-lengths than elsewhere, and it is possible that the avoidance of violet light as shown in these experiments is of significance in explaining the avoidance of sunlight under certain conditions, but it is more probable that temperature is the dominating factor in this reaction.

IV. Summary and Conclusions

1. Of the temperature conditions capable of being tested in the gradient, the temperature of the substratum calls forth the most definite response. In addition to the

indication of an optimum by the movements of the animal, definite motor responses of a specialized character (burrowing) are made to certain temperature conditions just above or just below this optimum. The temperature of the air calls forth similar reactions but not as readily or as definitely as that of the soil, the reaction to the former being overshadowed by the response to the latter when a difference exists. The temperature of the substratum is evidently of very great importance in the daily movements of the horned lizards, and probably plays an important rôle in the control of distribution. The temperature of the soil is probably also of great importance in connection with the deposition and hatching of the eggs in those species which are oviparous. The differences between the optimum temperatures of the various species considered are in the direction and of the magnitude of the temperature differences normal to their respective habitats. While the limits of temperature variation favorable for the completion of the life cycle of the animal could not be subjected to experiment of the type here used, it is evident that at least the minimum is of great importance in connection with the phenomena of hibernation, and the maximum is probably of similar importance in relation to the estivation which takes place more or less regularly.

2. In the gradient of the evaporating power of air definite responses were obtained only in the case of one species (*Phrynosoma modestum*), and here only when the gradient was steep. The daily and seasonal variation in this factor is very large in the natural habitat. The reactions of the animals to temperature changes act in such a way as to prevent the exposure of the organism to excessive desiccation. The effect of soil moisture is felt indirectly, through the alteration of the temperature and the texture of the soil, the latter of which is important in relation to the burrowing habit. It is probable that there is a certain minimum water content of food, below which the animal can not survive. This must be very

low, however, considering the character of the normal food. The excretion of water is reduced to a minimum by the character of the nitrogenous excreta, which are almost exclusively in the form of insoluble uric acid.

3. An important factor in the distribution of these animals is the texture of the soil, which must be suitable for burrowing, as this is the reaction of the animal to unfavorable conditions generally, and specifically to temperatures inducing hibernation and estivation. The soil texture is affected adversely by increases in moisture content, and by increases in the amount of vegetation present. The color of the soil is probably important from the standpoint of invisibility and it is probable that there is some degree of approximation of the color of the animal to that of the substratum. It is difficult to see how this fact could be of much use to the animals, especially in the case of such profusely armored species as *Phrynosoma cornutum*.

4. The rôle of light in the daily and seasonal life of the horned lizards has not been shown, although they are positively phototactic and avoid extremes in a color gradient. The optimum in this gradient lies in the green and in the yellow. This may be correlated with the predominant colors of soil and vegetation in the natural habitat.

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